

THE ANATOMICAL STRUCTURE AND SYSTEMATIC POSITION OF *PENTABLASTUS* (BLASTOIDEA) FROM THE CARBONIFEROUS OF SPAIN

by K. A. JOYSEY and A. BREIMER

ABSTRACT. *Pentablastus supracarbonicus* Sieverts-Doreck was described originally from only two specimens. The collection of over twenty additional specimens has now made possible a more detailed description, including an account of the internal structure. Optical discontinuities in the calcite have been used to detect boundaries between the component plates, and serial sections have been prepared by the new annular sawing technique at 0.35 mm. intervals. These methods have revealed several unexpected features, including an optical discontinuity between the body and the limbs of each radial plate. The posterior deltoid is divided, and all the deltooids have a concealed vertical limb lying internally to the radials. There are basal pits on the floor of the thecal cavity. Although the under-lancet plate is a distinct structural unit, it is divided by an optical discontinuity along the mid-line of the ambulacrum. Each half of the under-lancet plate is continuous adorally with a hydrospire-plate, so providing direct evidence in favour of a compromise solution to the long standing controversy on the nature of the under-lancet plate in blastoids.

While making comparisons with other forms it has been found that the posterior deltoid of *Acentrotremites* is divided, and that the subradial plate of this genus is merely a concealed internal limb of the deltoid. *Pentablastus* and *Orophocrinus* show a close similarity in the form of the under-lancet plate, and in the relationship between the hydrospire-folds and the hydrospire-clefts. A distinction is made between hydrospire-slits and hydrospire-clefts, the latter being present in *Pentablastus* and some species of *Orophocrinus*, including the type species. It is suggested that those species of *Orophocrinus* which do not possess hydrospire-clefts should be removed from this genus. *Orophocrinus* is itself removed from the Phaenoschismidae and placed in the same family as *Pentablastus*, for which family the name Orophocrinidae Jaekel has priority over Pentablastidae Sieverts-Doreck. Amended diagnoses are given.

THE blastoid species *Pentablastus supracarbonicus* Sieverts-Doreck was described originally on the basis of two specimens from the Carboniferous limestone of Rabanal, in the province of Palencia, Northern Spain. Sieverts-Doreck (1951) recognized this species as the only known representative of a new family, the Pentablastidae, within the subclass Fissiculata.

More specimens of *Pentablastus* have now been collected and the material at present available consists of twenty-two individuals and several additional fragments. All the specimens figured in the present paper have been deposited in the Rijkmuseum voor Geologie en Mineralogie, Leiden, Holland. The Leiden catalogue numbers 102451-76 correspond serially to our reference numbers 1-26, which are marked on the specimens. In the present paper, these numbers are given in brackets to facilitate reference to individual specimens, and to indicate those specimens which well display particular characters.

Most of the new material was collected at Rabanal, near Cervera de Pisuerga, but three specimens came from other localities, near Orbó (17), the valley of El Ves (18) and Perapertu (22) respectively, all within the province of Palencia. The local geology has been described by de Sitter (1955). It has been suggested that the Rabanal limestone is of Westfalian age (Quiring 1939), but investigation of the fusulinid fauna suggests that it is probably of Namurian age (A. C. van Ginkel, personal communication).

The present description of *Pentablastus* is supplementary to that given by Sieverts-Doreck (1951). The relatively large number of specimens at our disposal has enabled us to make some additional observations on the anatomical structure, and we have found it necessary to revise the systematic diagnosis. Comparisons between the hydrospire system of *Pentablastus* and that of a number of other blastoid genera has led us to make a reappraisal of its systematic position.

TECHNIQUES

(a) *Optical properties of the component plates*

It is well known that the calcite in each component plate of an echinoderm skeleton is usually orientated as a single crystal. The literature on this subject has been reviewed recently by Raup (1959). With fossil echinoderms it is often possible to detect plate boundaries by differences in the reflecting properties of the surfaces of the adjacent plates (Pl. 67, figs. 4, 6).

Before we had thin sections available, we coarsely ground some plane surfaces transversely to the ambulacra, on some of the broken specimens. It was then possible to detect differences in the optical orientation of the component plates by means of their different reflecting properties, when viewed in ordinary light. This effect can be accentuated by increasing contrast during photography (Pl. 68, figs. 5, 6).

Lucas (1953) used a polarizing microscope to distinguish plate boundaries in thin sections of blastoids, and determined the orientation of the crystallographic axis of each of the component plates. In his work on *Cryptoschisma*, Lucas found that the radial, deltoid, and lancet plates all contribute to the formation of the hydrospire-folds.

In *Pentablastus*, we have found (i) an optical discontinuity between the body of the radial and its two limbs (p. 475); (ii) the posterior deltoid is divided (p. 475); (iii) an

EXPLANATION OF PLATE 66

Pentablastus supracarbonicus Sieverts-Doreck.

- Fig. 1. Ambulacral view of adult. $\times 1.5$. Spec. 4, Leiden No. 102454. (Cambridge photo.)
 Fig. 2. Ambulacral view of young individual. $\times 3$. Spec. 1, Leiden No. 102451. (Cambridge photo.)
 Fig. 3. Adoral region of ambulacrum of young individual, showing parallel rows of brachiole pits on widening series of side-plates in region of hydrospire-clefts. $\times 6$. Spec. 2, Leiden No. 102452. (Leiden photo.)
 Fig. 4. Summit view of young individual, showing large hypodeltoid (subanal) in posterior interradius, and narrow limb of epideltoid (lateral) on each side of hypodeltoid. $\times 5$. Spec. 1, Leiden No. 102451. (Leiden photo.)
 Fig. 5. Adoral region of ambulacrum of weathered specimen, showing broken lancet lying in groove on under-lancet. On right side, in region of hydrospire-cleft, the widened lancet covers the adoral spur of the under-lancet (now hydrospire-plate). $\times 7$. Spec. 24, Leiden No. 102474. (Cambridge photo.)
 Fig. 6. Transverse section of an interambulacrum near the adoral limit of the hydrospire-folds. Note the vertical limb of the deltoid (reflecting) lying within the radial plates. The alternating strips of radial and deltoid material indicate a crenulated surface of contact between the radial and the horizontal limb of the deltoid. Each of the hydrospire-sacs lies within a strip of radial material. $\times 11$. Spec. 5, section 5 (top), Leiden No. 102455. (Leiden photo.)
 Fig. 7. Naturally weathered transverse section of ambulacrum near equatorial region, showing narrow lancet lying in groove on wide top of under-lancet, and side-plates resting partly on each. Note median division of under-lancet. $\times 14$. Spec. 11, Leiden No. 102461. (Leiden photo.)



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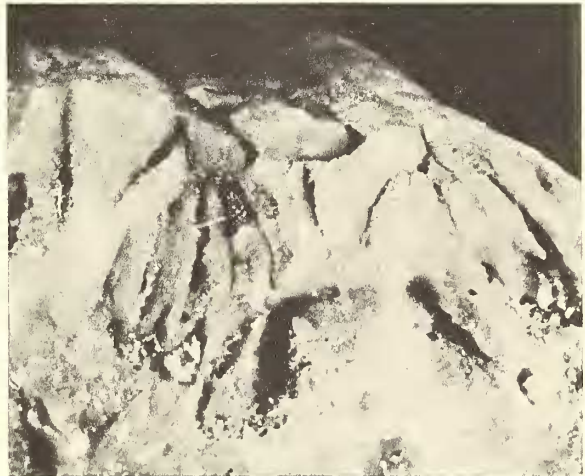
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optical discontinuity between the two halves of the under-lancet plate (p. 479). All of these observations were made using the 'reflection' method in ordinary light, and subsequently confirmed in thin section with a polarizing microscope (e.g. Pl. 67, fig. 5).

While the value of optical discontinuities in the elucidation of blastoid anatomy is well established, we have found it necessary to use the method with caution on the present material. Although most of the optical properties of the component plates represent their primary structure, there can be no doubt that both optical continuities and discontinuities can be the product of secondary recrystallization. It has not always been possible to make consistent observations between the several ambulacra of the same individual, and so it has proved necessary to weigh the evidence provided by several specimens.

(b) *Serial sections*

Serial drawings and photographs prepared by serial grinding are commonplace in palaeontology (e.g. Pl. 68, figs. 1-4) but their preparation usually involves the total loss of the specimen. This method clearly has the disadvantage that it is impossible to check back to critical sections. On the other hand, thin sections prepared from rock slices cut by the conventional diamond-armed circular-saw cannot be obtained sufficiently close together for detailed anatomical studies. This is because the original rock slice must be fairly thick in order that it should not be shattered by lateral movements of the saw blade during the cutting process.

Thwaites and Sayers (1955) have described a new saw which has overcome this difficulty. It consists of a thin annulus of metal which is clamped round its outer edge to tension the blade against deflexion. The inner edge is armed with diamond dust as the cutting agent, and the material to be cut is mounted within the annulus, and can be traversed into contact with the cutting edge. In suitable material it is possible to cut a series of slices, each only 0.3 mm. thick, separated by a series of parallel saw-cuts of the same width as the slices, and so only half of the material is destroyed in the cutting process. This machine was originally designed to cut thin plates of quartz for use as piezoelectric vibrators in radio components, and it is now manufactured under patent by Caplin Engineering Co. Ltd., Ipswich. Credit is due to Mr. C. F. Sayers for recognizing the potentiality of this machine for cutting serial sections of fossils.

Two specimens of *Pentablastus* (5, 22) have been cut by the annular-saw method. Prior to cutting they were embedded in an artificial matrix consisting of a mixture of Marco Resin and plaster of Paris. Some difficulty was encountered with one of the specimens, partly due to calcite cleavage and partly because it was hollow. These difficulties were largely overcome by impregnating with Marco Resin after the cavity had been exposed by cutting the first few sections.

The sections of *Pentablastus* range in thickness from 0.3 mm. to 0.4 mm., and are separated by saw-cuts of comparable width, and so by examining both sides of each slice it has been possible to achieve permanent serial sections at approximately 0.35 mm. intervals. These have been examined under a high-power binocular microscope by shining an intense transmitted light through the thickness of the slice. By this method it is possible to trace sutures through the slice and observe the direct connexion between the two surfaces. Nevertheless, it is possible to obtain separate photographs of the two sides by using a short depth of focus, and partly relying on scattering of light within the thick-

ness of the slice to blur the image of the opposite side (Pl. 69, figs. 1–10). It will be appreciated that it has been necessary to photographically reverse (mirror image) alternate pictures in order to make a continuous series, so that some surfaces actually photographed from below have been printed as though viewed from above.

We are indebted to both Mr. C. F. Sayers and Mr. R. Jones for embedding the specimens and cutting the serial sections and to the Post Office Engineering Department for permission to use an Annular Sawing machine for cutting this material. We should also like to thank Mr. B. F. M. Collet and Mr. J. Hoogendoorn of Leiden, and Mr. R. D. Norman of Cambridge, for their invaluable assistance with the photography and illustrations.

DESCRIPTION

Size and shape. The smallest complete specimen is 14 mm. high and 11 mm. in diameter, and the largest specimen is 30 mm. high and 26 mm. in diameter. The ratio diameter/height ranges from 0.70 to 0.96 (based on eight specimens), and diameter is less than height in all the other specimens in which their relationship can be observed.

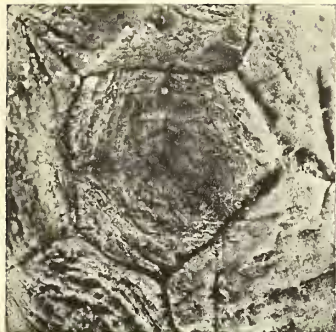
The general form of specimens of different size is shown in Plate 66, figs. 1 and 2, where different scales of magnification have been used to bring the two specimens to nearly the same apparent size. The younger individual (fig. 2) is ovoid in outline, whereas the adult (fig. 1) has a pear-shaped profile.

Stalk. A small remnant of the stalk is preserved on one of the smaller specimens (diameter 13 mm.), where a single columnal plate lies within the basal concavity of the

EXPLANATION OF PLATE 67

Pentablastus supracarbonicus Sieverts-Doreck.

- Fig. 1. Basal region of weathered specimen, showing three basal plates lying within basal concavity, bounded by radial plates. $\times 7$. Spec. 2, Leiden No. 102452. (Leiden photo.)
- Fig. 2. Same region as previous photograph, on a more deeply weathered specimen, showing basal plates surrounded by the basal pits of thecal cavity, situated on interradian-basal sutures. $\times 7$. Spec. 23, Leiden No. 102473. (Cambridge photo.)
- Fig. 3. Transverse section through basal region of large incomplete specimen, showing basal plates (reflecting) surrounded by basal pits of thecal cavity, some partly filled with matrix. (The basal cavity has been artificially deepened, and the small cavity filled with matrix is part of a 'worm'-burrow.) $\times 2.5$. Spec. 5, section 20 (bottom); Leiden No. 102455. (Cambridge photo.)
- Fig. 4. Oblique radial view, showing optical discontinuity between body of radial (reflecting) and limbs of radial. Note lappet of radial body in contact with tip of ambulacrum. $\times 3$. Spec. 3, Leiden No. 102453. (Cambridge photo.)
- Fig. 5. Longitudinal section through basal region, viewed between crossed nicols, showing on left the optical discontinuity between body of radial (light) and limb of radial (dark). Note matrix in basal concavity, basal plates (black), and on right the basal pit of thecal cavity. $\times 6$. Spec. 16, Leiden No. 102466. (Leiden photo.)
- Fig. 6. Side view, showing same features as fig. 4 (above). $\times 3$. Spec. 3, Leiden No. 102453. (Cambridge photo.)
- Fig. 7. Transverse section of radial just beyond tip of ambulacrum, showing main part of radial body (lower dark), the radial limbs (both reflecting) and the lappet of the radial body (upper dark). Note tip of lancet, under-lancet, and hydrospires completely embedded in radial. (The uppermost dark area is a bubble in the embedding medium.) $\times 8$. Spec. 5, section 19 (top); Leiden No. 102455. (Cambridge photo.)
- Fig. 8. Oblique radial view of small weathered specimen, showing line of division between radial body (infraradial) and radial limb (supraradial). Note difference in cleavage between the two regions. $\times 3.5$. Spec. 2, Leiden No. 102452. (Cambridge photo.)



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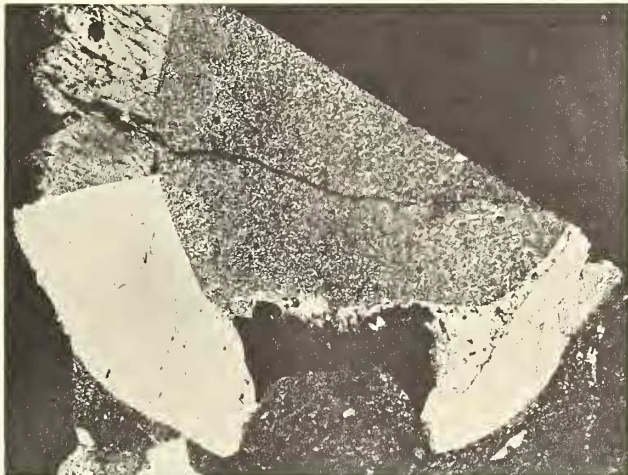
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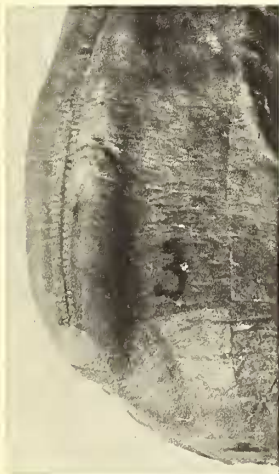
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theca (1). It almost covers the basal plates, was probably circular prior to weathering, and has a maximum diameter of 3·1 mm.

Basal plates. Three basal plates form a pentagonal area lying entirely within the basal concavity, the margin of which is formed by the radial plates (Pl. 67, fig. 1). As is usual in blastoids, one of the basal plates is smaller than the other two, and it has been confirmed, both on a whole specimen (23) and in serial sections (5, 22), that the small basal plate is situated in the normal position, the left anterior interradius, as seen in basal view.

Radial plates. As described by Sieverts-Doreck the radial plates are large and form the greater part of the theca. In large specimens the ambulacra extend five-sixths of the total height, and so the body of the radial plate is mainly on the underside of the theca. In contrast, in small specimens the ambulacra extend only three-quarters of the total height, and so the convex body of the radial plate forms a relatively larger part of the side of the theca (Pl. 66, figs. 1, 2). The margins of the radial sinus are swollen alongside the lower (aboral) part of each of the ambulacra. Serial sections show that this swelling of the external surface is associated with a general increase in thickness of the radial plates in this region (Pl. 69, figs. 6–10).

There is an optical discontinuity between the body of the radial and its limbs (Pl. 67, figs. 4–7). The line of demarcation between the two regions is not represented by a suture on the surface, except in weathered specimens (Pl. 67, fig. 8). It is almost horizontal on the flanks of the theca, but is characteristically curved upwards near the tip of the ambulacrum, so that a small lappet of the radial body overlies the radial limbs in this region. The tip of the ambulacrum is always in contact with the body of the radial.

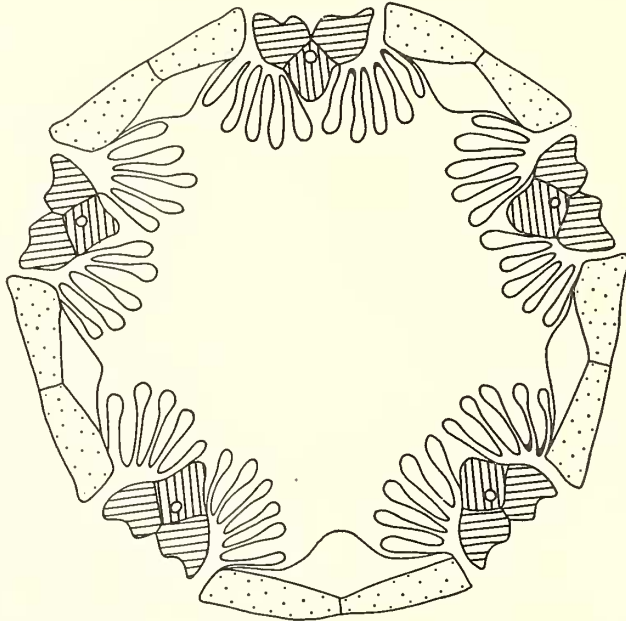
This optical discontinuity suggests a composite origin of the radial plate in *Pentablastus*. We propose to name the lower part (radial body) the infraradial region, and the upper parts (radial limbs) the supraradial regions. The supraradial regions of *Pentablastus* have a similar disposition to the bibrachial plates of *Blastoidocrinus*, but insufficient is known to conjecture on possible homologies. While it is possible that only the infraradial region of *Pentablastus* is homologous with the radial plate of other blastoids, it seems more likely that the whole of the radial region of *Pentablastus* is homologous with the radial plate. Clearly these subdivisions of the radial plate must be sought in other genera.

Weathered specimens (6, 18, 23) and serial sections reveal the presence of five deep pits on the floor of the thecal cavity, situated at the junction of the interradiial sutures and the radial-basal suture, similar to the pits for the chambered-organ in crinoids (Pl. 67, figs. 2, 3, 5).

Deltoid plates. As described by Sieverts-Doreck, the deltoid plates are nearly horizontal, and form the summit of the theca. This description, however, applies only to that part of the deltoid which is visible in external view. Examination of weathered specimens (3, 7, 14, 15, 24) and serial sections (Pl. 69, figs. 1–7) has revealed that the deltoid plate also has an almost vertical limb, which extends downwards internally to the radial plates (text-fig. 1). This concealed part is nearly equal in size to the exposed horizontal limb of the deltoid. In the posterior interradius the concealed limb of the deltoid extends more than one third of the total height of the theca, and in the other interradii it extends for one quarter of the total height.

The upper surface of the horizontal limb of the deltoid plates is characterized by a fairly deep, median, elongated depression, but in the posterior interradius this depression is separated from the aboral margin of the anus by a transverse ridge.

We find that the posterior deltoid is divided, but this condition is not immediately obvious on some specimens. A few of the deeply weathered specimens have two sutures extending from the lower (aboral) margin of the anus to the lower border of the deltoid plate (23, 24). These sutures divide the area of the deltoid below the anus into three



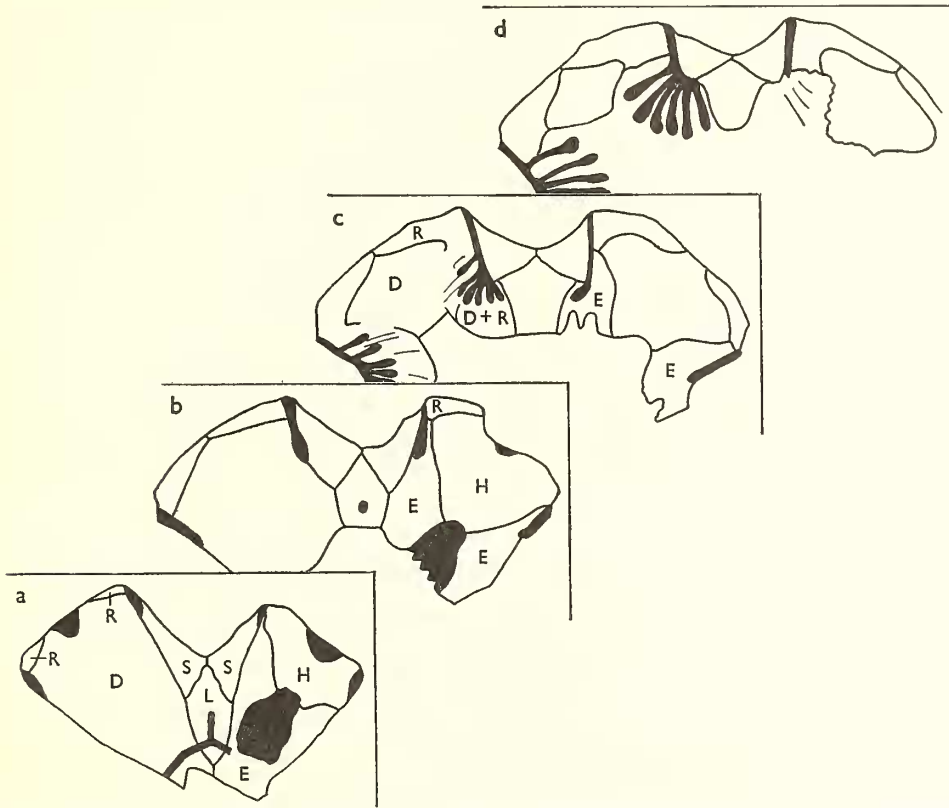
TEXT-FIG. 1. *Pentablastus supracarbonicus*. Transverse section of young specimen, in the middle region of the hydrosphere-clefts, just above the adoral limit of the hydrosphere-plates. Note the vertical limb of the deltoid (not shaded) lying internally to the radial plates (stippled). Lancet plates (vertical hatch); side-plates (horizontal hatch). $\times 9$. Spec. 17, Leiden No. 102467.

regions of approximately equal width—a subanal region and two lateral regions. In contrast, on an unweathered specimen (1), the central subanal plate occupies nearly the whole deltoid area, and it overlaps the lateral regions to such an extent that they are reduced to a very narrow strip on each side (Pl. 66, fig. 4). The extension of these lateral regions under the subanal plate has been confirmed by serial sections which show oblique sutures between the subanal plate and the lateral regions of the deltoid (text-fig. 2*a-c* and Pl. 69, figs. 1–3).

No suture has been observed between the two lateral regions of the deltoid in the small area of deltoid plate above (oral to) the anus (text-fig. 2*a*), and so these two lateral regions are, in fact, two limbs of a single plate. Using Wanner's terminology (1940), this plate can be referred to as an epideltoid, and the subanal plate is the hypodeltoid.

Horizontal sections across the theca near the adoral tip of the hydrosphere-folds (text-fig. 2, on the left side of each section, at a level between *b* and *c*) reveal a complicated

pattern in the form of each deltoid plate. This may be aptly described as a 'cedar-tree' pattern (text-fig. 3 and Pl. 66, fig. 6). The crown of the 'cedar' is formed by the vertical limb of the deltoid and the trunk is the horizontal limb of the deltoid. At this level, extensions of the radial plates underlie each side of the horizontal limb of the deltoid,



TEXT-FIG. 2. *Pentablastus supracarbonicus*. Nearly horizontal sections through an ambulacrum (V) and the adjacent interambulacra, showing the division of the posterior deltoid into hypodeltoid (H) and epideltoid (E), and the relationship between the radial (R), and deltoid (D) plates. Lancet (L); side-plates (s). Sections at irregular intervals selected from a series at approx. 0.35 mm. interval. All drawn as though viewed from above. $\times 5$. Spec. 5, Leiden No. 102455. For additional detail see Pl. 69, figs. 1-4, where 1 = a; 2 = b; 3 = c; 4 = d.

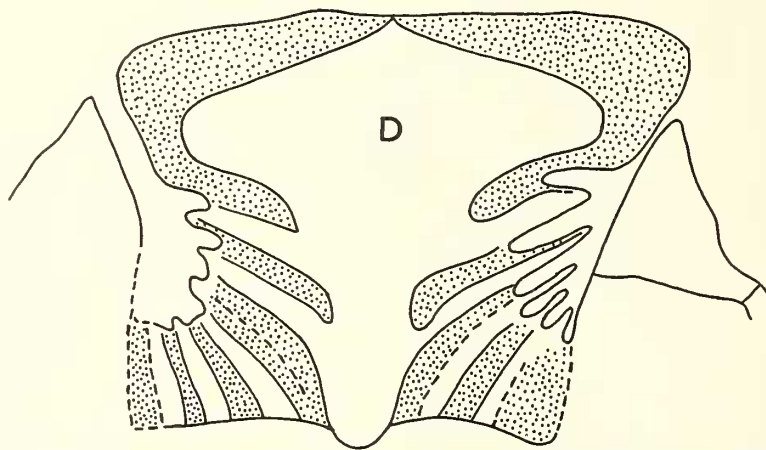
and the lower branches of the 'cedar' are formed by a crenulated surface of contact between these plates, resulting in alternate strips of radial and deltoid material. Each of the strips of radial material is associated with the adoral tip of a hydrosfire-fold. (The hydrosfire openings have the form of a single hydrosfire-cleft on each side of the adoral region of the ambulacrum. They extend adorally beyond the limit of the hydrosfire-folds, and reach a level just above the radial-deltoid suture, as seen on the exterior of the theca (p. 481).)

Side-plates. The ambulacra are long and narrow. Each ambulacrum, at its lower (aboral) end, is raised on a prominence relative to the interradian areas, but it passes into a

shallow groove when traced towards the mouth. Even in the raised region the side-plates lie in a furrow relative to the swollen margin of the radial sinus (Pl. 66, figs. 1, 2).

The adjacent rows of side-plates meet in the mid-line of each ambulacrum throughout its length, and so the lancet plate is not exposed in a perfect specimen. There are fifty side-plates in each row in a specimen 16 mm. high (1) and about ninety in a specimen 30 mm. high (3). A small triangular outer side-plate is associated with each side-plate, overlying its top outer corner and separated from it by an oblique suture (8).

There is a single brachiole pit on each of the side-plates. Although the ambulacra



TEXT-FIG. 3. *Pentablastus supracarbonicus*. Horizontal section through an interambulacrum near the adoral limit of the hydrosfire-folds, showing the 'cedar-tree' pattern of the deltidial plate (D). Radial plates stippled. For explanation see text. $\times 15$. Spec. 5, section 5 (top); Leiden No. 102455. (Composite drawing made from several photographs, one of which is illustrated on Pl. 66, fig. 6.)

EXPLANATION OF PLATE 68

Pentablastus supracarbonicus Sieverts-Doreck

Figs. 1-4. Series of nearly transverse sections of young specimen, obtained by parallel grinding and photographed at intervals. $\times 7.5$. Spec. 17, Leiden No. 102467. (Leiden photos.)

Fig. 1. Adoral region of hydrosfire-clefts, showing adoral end of hydrosfire-folds at slightly different levels of section.

Fig. 2. Middle region of hydrosfire-clefts, showing the hydrosfire-folds opening independently into each hydrosfire-cleft.

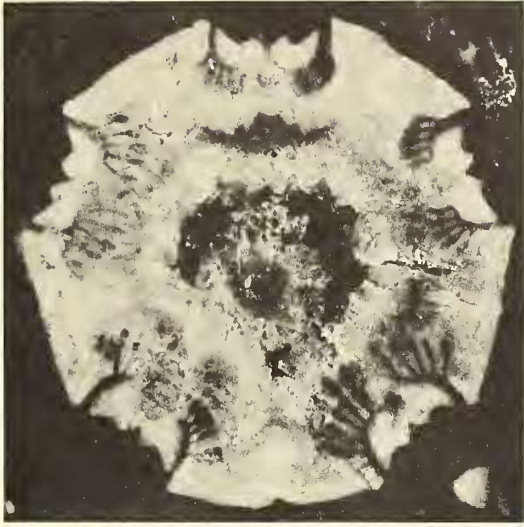
Fig. 3. Aboral region of hydrosfire-clefts, showing hydrosfire-folds opening into a common hydrosfire-canal. Note slight thickening of thecal wall between hydrosfire-folds.

Fig. 4. Dorsal to hydrosfire-clefts, showing thickened wall of theca enclosing bases of hydrosfire-folds, and under-lancet lying between the two groups of hydrosfires.

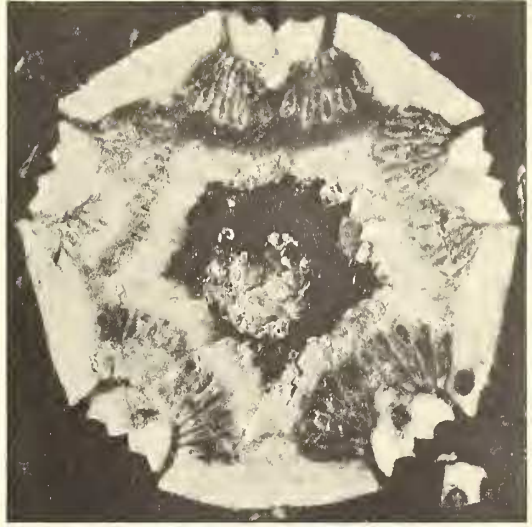
Figs. 5-6. Obliquely transverse sections of ambulacra, obtained by coarse grinding, and photographed in ordinary light. Differences in reflecting properties accentuated by increasing contrast during photography. Spec. 25, Leiden No. 102475. (Cambridge photos.)

Fig. 5. Equatorial region of ambulacrum, showing optical discontinuity between the two halves of the under-lancet. The secondary infilling of the hydrosfire-folds has formed in optical continuity, on left, with the adjacent half of the under-lancet, and on right, with the lancet. $\times 14$.

Fig. 6. Aboral region of ambulacrum, showing lancet resting on under-lancet plate, and the almost complete enclosure of the hydrosfire-folds within the wall of the theca. $\times 12$.



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change in width, the distance between the two rows of brachiole pits remains constant. In consequence, the outer margins of the ambulacral plates are unsculptured in the upper part of the theca (Pl. 66, figs. 3, 4).

Lancet plate. In a specimen in which the side-plates and outer side-plates have been removed (Pl. 66, fig. 5), it may be seen that the lancet plate extends along the entire length of the ambulacrum. Within the radial sinus the lancet plate is nearly parallel sided and does not occupy the whole width of the ambulacrum, but it gradually widens in the region of the hydrospire openings (7), and finally, in the region between the deltoids it occupies the whole width of the ambulacrum. A longitudinal canal perforates the lancet throughout its length, and at the adoral end connects with a ring canal lying within the deltoid plates (text-fig. 2a).

The exterior surface of the lancet plate has a crest along its mid-line throughout its length, underlying the suture separating the adjacent rows of side-plates. These lie on each side of the crest, in a shallow groove, which is sculptured to receive the individual side-plates.

The inner surface of the lancet plate shows several changes in form when traced from the lower (aboral) end of the radial sinus towards the mouth. These changes in the shape of the cross-section of the lancet plate can be observed in the serial sections illustrated (text-figs. 2, 4; Pl. 69), but it must be noted that at the top of the theca the lancet plate curves over towards the mouth and so these horizontal sections cut the lancet at an oblique angle, and give an exaggerated impression of its thickness relative to the width. At the lower end, the inner surface of the lancet is slightly convex, but it gradually becomes more convex, and in the region just aboral to the hydrospire-clefts there is a median ridge with a shallow depression on each side. In the adoral region of the hydrospire-clefts the lancet has an almost flat inner surface, so that it has a pentagonal cross-section. Traced farther towards the mouth the pentagonal cross-section persists, but the thickness of the lancet increases relative to its width.

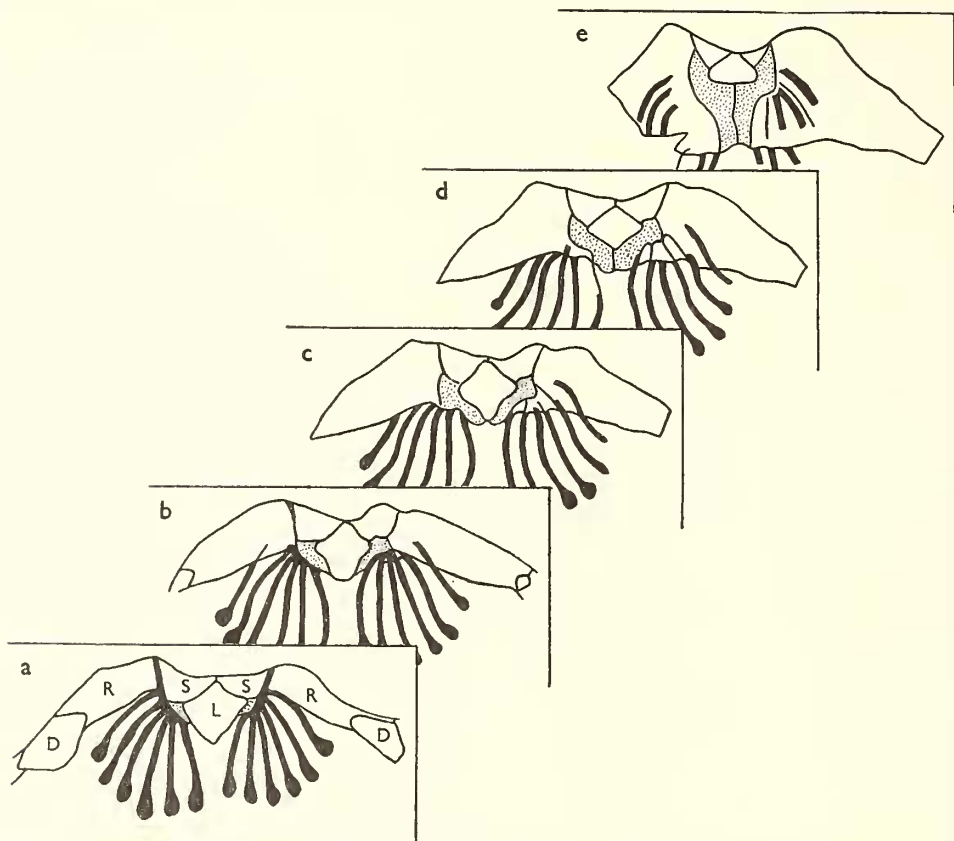
Under-lancet plate. Within the radial sinus the lancet plate rests upon an under-lancet plate which is wider than the lancet and so is exposed in exterior view when the side-plates have been stripped off. A suture marks the line of contact between the under-lancet and the adjacent radial plate (Pl. 66, figs. 5, 7). The surface of the under-lancet has a groove along its mid-line to receive the convex lower surface of the overlying lancet, and the side-plates rest partly on the under-lancet and partly on the lancet itself.

The under-lancet occupies the whole space between the hydrospire groups, its lateral margin being determined by the position of the innermost hydrospire-fold in each group. The inner surface of the under-lancet is almost flush with the inner surface of the radial plate on each side, and both increase in thickness towards the lower (aboral) part of the ambulacra (Pl. 69, fig. 10).

Although the under-lancet plate forms a distinct structural unit, it consists of two parts which join along a suture in the mid-line of the ambulacrum, and they are not in optical continuity with one another (Pl. 68, fig. 5). These two halves of the under-lancet are continuous with a pair of hydrospire-plates. Direct evidence of this interpretation has been obtained from serial sections (text-fig. 4a-e; Pl. 69, figs. 6-10). At the level of the hydrospire-clefts, there is a discrete hydrospire-plate lying on each side of the lancet, in the depressions on each side of the median rib on its inner surface. Aborally to the

hydrosfire-clefts these hydrosfire-plates increase in size and come into contact with one another under the lancet plate, and other sections lower down the ambulacra show a progressive thickening to form an under-lancet plate.

At first sight, on the assumption that the two halves of the under-lancet might be



TEXT-FIG. 4. *Pentablastus supracarbonicus*. Nearly horizontal sections through an ambulacrum (IV) and the adjacent interambulacra, showing the hydrosfire-plates (stippled) coming into contact in the mid-line, and forming an under-lancet plate in the region aboral to the hydrosfire-clefts. Deltoid (D); lancet (L); radial (R); side-plates (s). Sections at irregular intervals selected from a series at approx. 0.35 mm. interval. All drawn as though viewed from above. $\times 5$. Spec. 5, Leiden No. 102455.

For additional detail see Pl. 69, figs. 6–10, where 6 = a; 7 = b; 8 = c; 9 = d; 10 = e.

derived ultimately from the same radial plate, the optical discontinuity between the two halves is unexpected. The situation is complicated, however, by the optical discontinuities within the radial plate itself. Apart from the optical difference between the body of the radial and the radial limbs, in some specimens the two limbs also differ from one another in their optical orientation. While optical discontinuity between the two limbs of the radial might be a product of mechanical distortion of the specimen, it is difficult to envisage that this could be the cause of optical discontinuity between the two closely contiguous halves of the under-lancet plate.

In a section of an apparently undistorted specimen the under-lancet halves situated on opposite sides of the same interradius are not in optical continuity with one another, and so it is unlikely that the under-lancet plates are derived ultimately from the deltoid plates. In many sections there is an optical difference between one half of the under-lancet, the adjacent radial limb and the adjacent deltoid, and so it would appear that the component parts of the under-lancet have an optical orientation of their own.

The compound under-lancet plate of *Pentablastus* occupies an analogous position to the under-lancet plate described by Etheridge and Carpenter (1886) in some species of *Pentremites* and *Orophocrinus*. The possible homology of these structures is discussed later.

Hydrospires. The hydrospire system is entirely internal. There are ten hydrospire groups, each consisting of six hydrospire-folds in the larger specimens, but only five folds in smaller individuals (Pl. 68, fig. 3; Pl. 69, fig. 6). The hydrospire-folds are relatively long and narrow, but inflated at the tips.

In the region of the hydrospire-clefts the individual hydrospire-folds open independently into a common longitudinal cavity which directly communicates with the exterior through the hydrospire-cleft itself (Pl. 68, fig. 1). Aborally to the level of the hydrospire-cleft there is a tendency for the hydrospire-folds to merge to form a common longitudinal canal which opens into the lower (aboral) end of the cavity within the hydrospire-cleft (Pl. 68, fig. 3). Throughout the rest of its length the longitudinal canal does not communicate directly with the exterior, its roof being sealed by the contact of the under-lancet and radial plate.

The hydrospire-clefts themselves are long narrow openings, one lying on each side of each ambulacrum, extending aborally from a position just above (oral to) the radial-deltoid suture, but confined to the oral quarter of the theca (Pl. 66, figs. 2-5). At its upper end the hydrospire-cleft widens slightly between the deltoid and the row of side-plates (1), but in this region it does not communicate directly with the interior cavity (text-fig. 2a, b; Pl. 69, figs. 1, 2).

At the level of the hydrospire-cleft the hydrospires are entirely free within the body cavity (Pl. 68, fig. 2), but below (aboral to) the hydrospire-cleft the radial plate thickens (Pl. 68, fig. 4), the under-lancet thickens, the spaces between the individual hydrospire-folds are progressively filled in, and so the hydrospire-folds become progressively enclosed within the wall of the theca (Pl. 68, fig. 5). At the lower (aboral) end of the radial sinus only the tips of the innermost (medial to the ambulacrum) fold of each group project into the body cavity (Pl. 68, fig. 6). Sections reveal that the tip of the lancet plate, the much reduced hydrospire groups and the under-lancet project into the body of the radial plate, beyond the externally visible end of the ambulacrum (Pl. 67, fig. 7).

SYSTEMATIC POSITION

Comparison with Acentrotremites

Sieverts-Doreck (1951) rightly drew attention to the superficial resemblance between *Acentrotremites* and *Pentablastus*, in the form of the theca, in the relative size, shape, and position of the deltoids, radials, and basals, and in the similar hydrospires. She also recognized the fundamental difference between the two forms, *Acentrotremites* having

spiracles and marginal pores, whereas *Pentablastus* has elongate hydrospire-clefts and no marginal pores. On this basis she retained *Acentrotremites* within the subclass Spiraculata and placed *Pentablastus* within the subclass Fissiculata.

Having re-examined the two specimens of *Acentrotremites* in the British Museum (Natural History) (E 782 and E 8256) and directly compared them with specimens of *Pentablastus*, it is possible to confirm all the similarities and differences described by Sieverts-Doreck, and also to note several additional characters in which the two genera may be compared and contrasted.

The median furrow on the deltoid of *Pentablastus* is remarkably similar to that described by Bather (1912) on *Acentrotremites*. Furthermore, in the deeply weathered specimen of *Acentrotremites* (E 782) a vertical limb of the deltoid may be seen to extend for a considerable distance beneath the radial plates, in a similar manner to that of *Pentablastus*.

Optical discontinuities in the posterior deltoid of one specimen of *Acentrotremites* (E 782) suggest that it is divided in a similar manner to that of *Pentablastus*. On each side of the anus, and extending slightly below its aboral margin, there are two small

EXPLANATION OF PLATE 69

Pentablastus supracarbonicus Sieverts-Doreck.

Figs. 1–10. Nearly horizontal sections of an ambulacrum and the adjacent interambulacra. 1–5 centred on Amb. V, and 6–10 centred on Amb. IV. Sections selected from a series at approx. 0.35 mm. interval, cut by the annular sawing technique. Photographed by transmitted light, and all printed as though viewed from above. $\times 7$. Spec. 5, Leiden No. 102455. (Cambridge photos.)

Fig. 1. Section 2 (top) near summit, with matrix in the grooves on the surface of the deltoids, and in the upper end of the hydrospire-clefts. Note (left) thin leaf of radial overlying outer corners of deltoid; (centre) matrix filled brachiole pits on nearly horizontal region of ambulacrum; (right) anus lying between descending limbs of epideltoid, with the hypodeltoid forming the main outer surface of the posterior deltoid region.

Fig. 2. Section 3 (bottom), 1.05 mm. below previous. Note (left) massive deltoid completely overlain by thin radials; (centre) matrix infilling canal within lancet; (right) epideltoid limbs completely internal, and outer corner of hypodeltoid overlain by radial.

Fig. 3. Section 4 (bottom). 0.70 mm. below previous. Note (left) upper limit of hydrospire-folds lying adjacent to deltoid of 'cedar-tree' form; (right) epideltoid limbs still present, and hypodeltoid covered by radial, except in weathered region.

Fig. 4. Section 5 (bottom), 0.70 mm. below previous, showing on each side the vertical limb of the deltoid completely covered by the radials. Note (left) hydrospire-folds suspended within thecal cavity.

Fig. 5. Section 6 (top), 0.35 mm. below previous, showing further reduction of deltoids and enlargement of hydrospire-folds.

Fig. 6. Section 7 (top), 0.70 mm. below previous, showing (right) hydrospire-folds opening into the hydrospire-cleft, adjacent to the adoral tip of the hydrospire-plate.

Fig. 7. Section 8 (bottom), 1.05 mm. below previous, showing a hydrospire-plate lying on each side of the lancet plate. Note (left) aboral termination of hydrospire-cleft.

Fig. 8. Section 10 (top), 1.05 mm. below previous, showing the hydrospire-plates just in contact beneath the mid-line of the ambulacrum.

Fig. 9. Section 10 (bottom), 0.35 mm. below previous, showing the under-lancet plate, formed by the union of the hydrospire-plates beneath the lancet plate. Note the proximal ends of the hydrospire-folds embedded within the wall of the theca.

Fig. 10. Section 12 (bottom) 1.40 mm. below previous, showing the increase in thickness of the radial and under-lancet plates. Note the mid-line suture between the two halves of the under-lancet plate.



